Characteristics and Modes of Origin of Weeds

H. G. BAKER

DEPARTMENT OF BOTANY, UNIVERSITY OF CALIFORNIA, BERKELEY, CALIFORNIA

Any article which purports to deal with weeds should begin with definitions of "weed" and "weedy." In my opinion, a plant is a "weed" if, in any specified geographical area, its populations grow entirely or predominantly in situations markedly disturbed by man (without, of course, being deliberately cultivated plants). Thus, for me, weeds include plants which are called *agrestals* by some writers of floras (they enter agricultural land) as well as those which are *ruderals* (and occur in waste places as well as along roadsides). It does not seem to me necessary to draw a line between these categories and accept only the agrestals as weeds (although this is advocated by some agriculturally oriented biologists) because in many cases the same species occupy both kinds of habitat. Ruderals and agrestals are faced with many similar ecological factors, and the taxa which show these distributions are, in my usage, "weedy."

In Berkeley, several students and I are studying the genecology and evolution of a number of tropical and temperate weeds. In particular, we are trying to find out what are the characteristics of these plants and which of their features are significant to their success. We are attempting to do this by making comparisons between the weedy taxa and closely related nonweedy taxa (cf. Baker, 1948, 1958, 1959, 1962; Adams and Baker, 1962; Cook, 1961; Nelson, 1962, 1964; Swanson, 1964). I should like to illustrate this work by reference to my own unpublished work with weedy and nonweedy species in the genera *Eupatorium* and *Ageratum*, of the Compositae. Both genera belong to the same tribe, the Eupatorieae.

The genus *Eupatorium* is a large one, with about 500 species. Only about three species out of that large number have been able to migrate, even with man's help, beyond the confines of the continent on which they arose. Consequently, there is interest in the comparison of two closely related species in the section Eximbricata—two species which are so

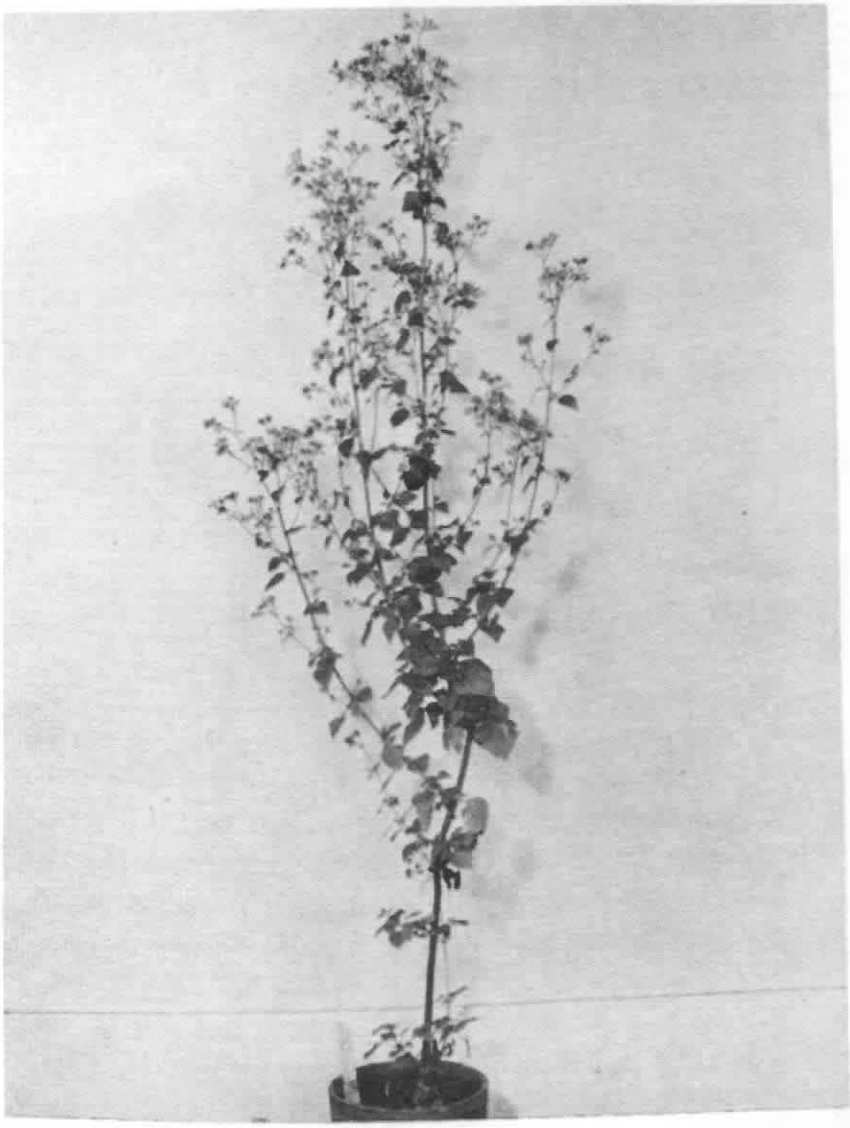

FIG. 1. Habit of a plant of perennial, nonweedy *Eupatorium microstemon* fr Costa Rica. Grown in greenhouse, Berkeley, California. Approx. 1.3 meters tall

closely related that herbarium botanists have usually considered th synonymous. One is a stay-at-home perennial in the uplands of Centr America and it has 20 pairs of chromosomes; the other is a weed rang from Guatemala to the West Indies and southward to Brazil and Pe It has crossed the Atlantic Ocean recently to become well established

West Africa. This weedy one has only four pairs of chromosomes. Both are filed in herbaria under the name *Eupatorium microstemon* Cass. (= *E. guadalupense* Spreng.), but should be recognized as separate taxa.

We have been comparing the growth requirements of these plants over several years, recently using growth chambers to find out their temperature and photoperiod preferences, and making hybrids and even amphidiploids from the hybrids. Detailed results will be published elsewhere.

The results may be summed up as follows. After germination, the nonweedy, perennial *Eupatorium microstemon* (Fig. 1) spends several months in the vegetative condition before it will flower (Table I). To induce flowering it must have short days and night temperatures which do not fall below about 50°F. This nonweedy perennial is highly self-incompatible, but it bears showy lilac or white flowerheads producing abundant pollen for cross-pollination. It shows little plasticity in the face of environmental variation. It wilts rather easily and is readily bleached by hot sunshine.

TABLE I

COMPARISON OF CHARACTERS OF WEEDY AND NONWEEDY *Eupatorium microstemon*

Eupatorium microstemon (weed)	*Eupatorium microstemon* (nonweed)
Plastic	Not very plastic
Annual	Perennial
Quick flowering	Slow to flower
Photoperiodically neutral	Short-day requirement
Self-compatible (autogamous)	Self-incompatible
Economical of pollen	Plentiful pollen production
$n = 4$	$n = 20$

By contrast, the weedy taxon is an annual (Table I; Fig. 2, left). It flowers well over a range of photoperiods, at least from 8 hours in length to more than 16-hours' duration. Its flower buds are initiated after a definite number of leaves have developed, the actual number seeming to depend upon temperature, crowding, and other features of the local environment. Its flowers are completely self-compatible, and they produce only enough pollen for self-pollination. There may be as few as two pollen mother cells per anther lobe, a considerable economy in pollen production compared with that of the nonweedy taxon. The weedy taxon is very plastic in the face of environmental variation (Fig. 3), and appears to be more drought resistant than the nonweedy perennial form.

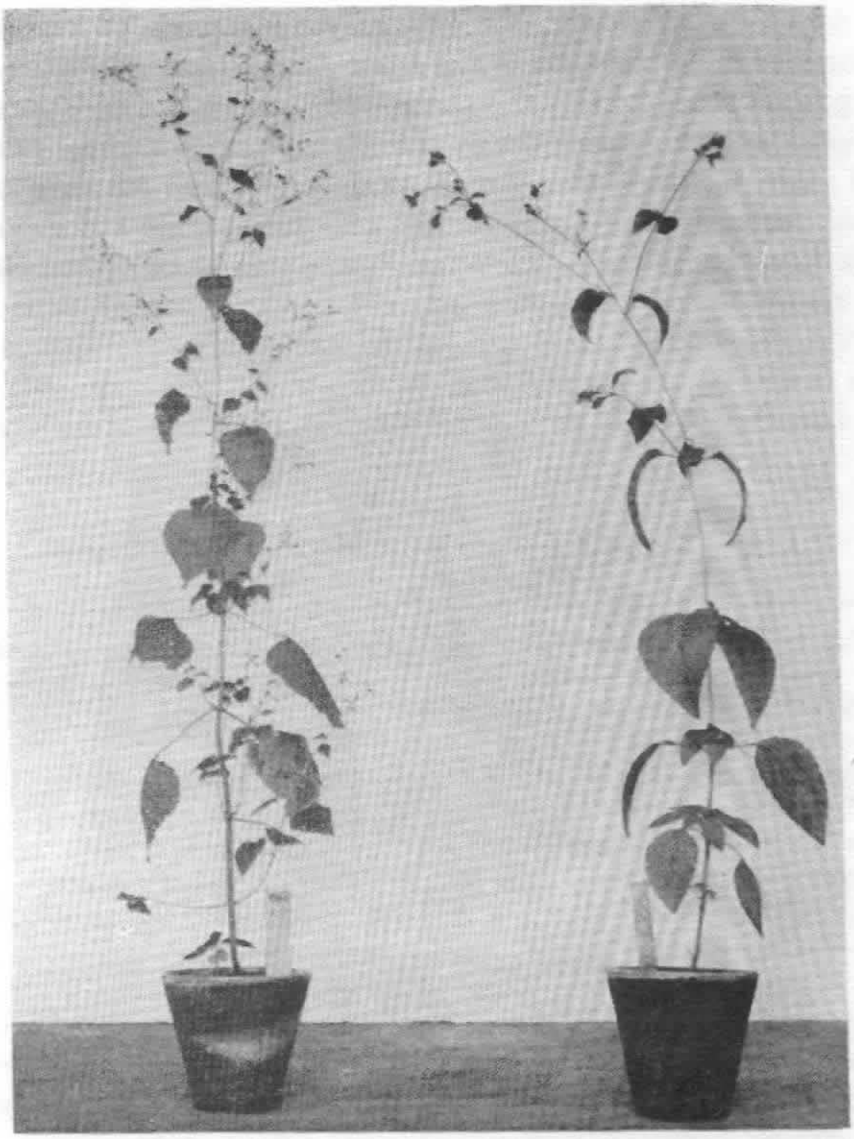

FIG. 2. *Left:* Plant of annual, weedy *Eupatorium microstemon* from Kibi, Ghana. Grown in greenhouse, Berkeley, California. Approx. 70 cm high. *Right:* Plant of *Ageratum conyzoides* from Legon, Ghana. Grown in greenhouse, Berkeley, California.

These are striking differences in life form, in physiology, and in reproductive biology and they compare rather well with what may be seen in a comparison of weeds and nonweeds in the next genus, the genus *Ageratum*. In *Ageratum* I include, for biosystematic reasons, the genus *Alomia* (for it differs only in a single character, the lack of a pappus, from the usually pappose *Ageratum*). In this genus, the nonweedy species are restricted to the New World tropics and subtropics.

Alomia microcarpa (Benth.) Robinson [which must revert to being called *Ageratum microcarpum* (Benth.) Hemsl. now that it is placed

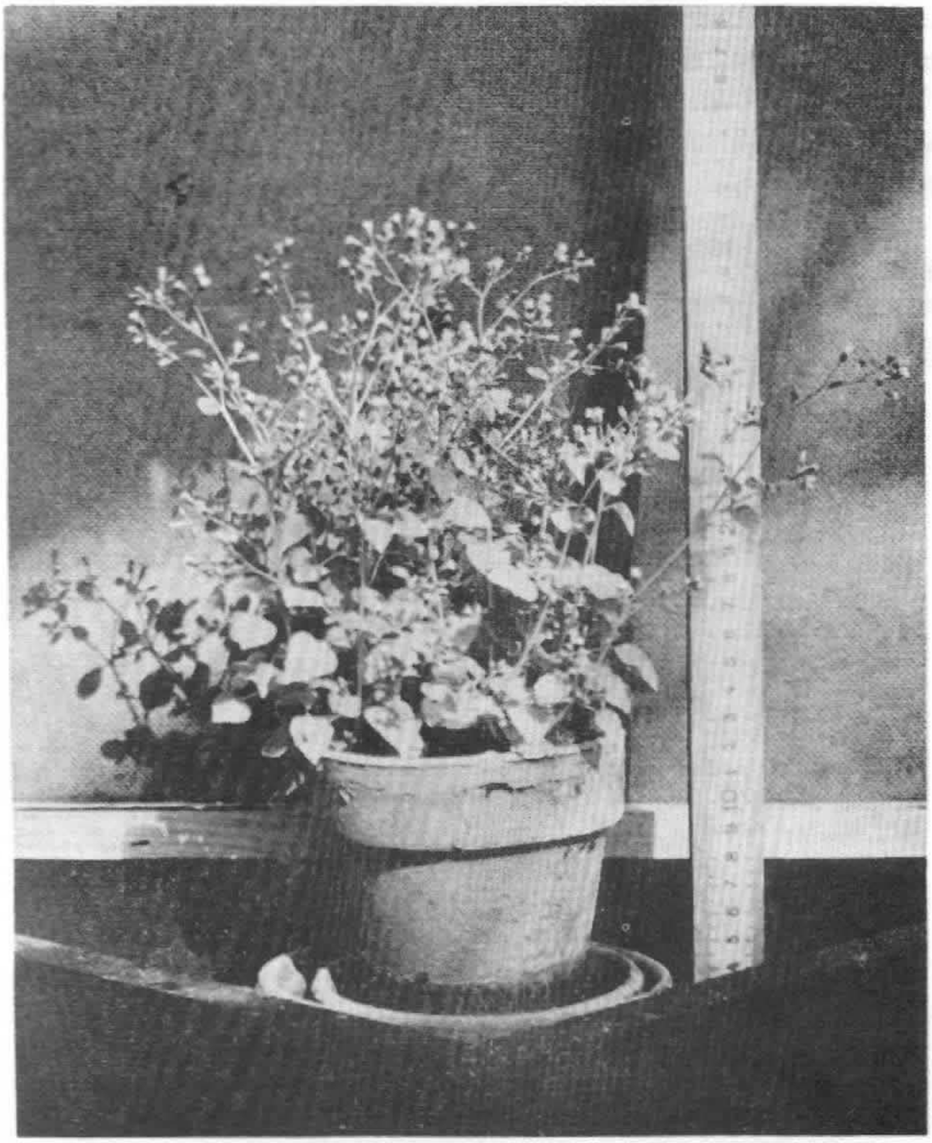

FIG. 3. Annual, weedy *Eupatorium microstemon* from Kibi, Ghana. Approximately 25 plants growing crowded together in 4-inch pot.

back in *Ageratum*] is found only in the highlands of Central America, where it grows in grass meadows. My material is diploid $(2n = 20)$, perennial, and often does not flower for a year after the germination of the original seed (Table II and Fig. 4). It needs a night temperature of about 50°F to bring it into flowering, even only 10° higher or lower will not do. It produces so much pollen from its showy blue flower heads (Fig. 5) that it is a potent cause of hayfever, but this pollen supply is needed because the plants are completely self-incompatible. These plants have rigid environmental requirements and there is no suspicion of weediness in them.

The taxonomic relationship of *Ageratum houstonianum* Mill. and *A. corymbosum* Zucc. is confused. They appear to differ from each other only in the shape of their pappus scales and both are completely interfertile with *A. microcarpum* (which lacks a pappus). Populations exist in Costa Rica which contain plants with each kind of pappus and others with none at all, so it may be that all of the so-called species belong to a single complex. They are being studied further.

Material matching the descriptions of *A. corymbosum* and *A. houstonianum* was obtained from European botanic gardens, for these taxa have been in cultivation in Europe since the second and third decades of the nineteenth century, respectively (Sims, 1815, 1823). The plants are slightly less rigid in their environmental requirements than *A. microcarpum* from Costa Rica and it is notable that *A. houstonianum* is recorded as having escaped from cultivation on a limited scale, for example, in Hawaii and on Okinawa. Nevertheless, many collections of "*A. houstonianum*" in herbaria and botanic gardens are misidentified and some certainly refer to the next species—the only one in the genus which has become a widespread weed.

TABLE II

COMPARISON OF CHARACTERS OF CLOSELY RELATED WEEDY AND NONWEEDY SPECIES OF *Ageratum*

Ageratum conyzoides (weed)	*Ageratum microcarpum* (nonweed)
Plastic	Not very plastic
Annual	Perennial
Quick flowering	Slow to flower
Flowers with low or high night temperatures	Flowers with rather low night temperatures
Self-compatible (autogamous)	Self-incompatible
Economical of pollen	Plentiful pollen production
$n = 20$	$n = 10$

This is *Ageratum conyzoides* L. (Fig. 2, right). Not only has the species escaped from the New World tropics, but it has become one of the commonest weeds throughout the warmer parts of the world.

It contrasts with the perennial, nonweedy species most strikingly (Table II). It is an annual and can go through its life cycle in less than 2 months. It will grow and flower over a range of temperatures from merely warm-temperate to strictly tropical, the flowering following, in some circumstances, after as few as two pairs of leaves have been formed. Consequently, unlike the perennials, it can colonize tropical lowlands, as well as tropical highlands. It appears to have no photoperiodic requirement for flowering and when it does flower, it is thoroughly self-compatible, even self-fertilizing. It produces an economical amount of pollen in its small heads.

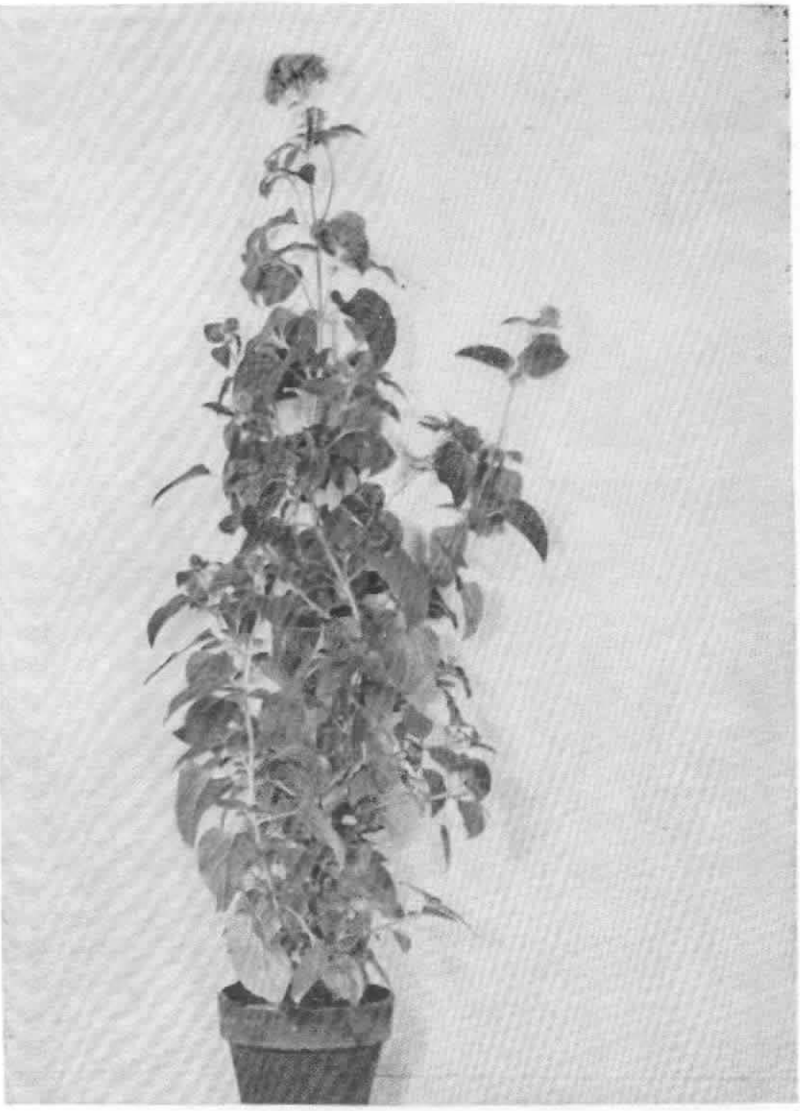

FIG. 4. Habit of a plant of perennial, nonweedy *Ageratum microcarpum* from Costa Rica. Grown in greenhouse, Berkeley, California. Approx. 1 meter high.

Plants of *Ageratum conyzoides* are extraordinarily plastic (Fig. 6)—very tiny plants with only a single flower head will mature seed in extreme conditions of crowding, waterlogging, or drought; on the other hand, they can grow to 2 feet in height with hundreds of flower heads in moist, well-lighted conditions. Its seeds will germinate in a wider range of conditions than those of the nonweeds. This is a wonderful weed, but it is the only really successful one in a genus of about 300 species.

Thus, in both *Ageratum* and *Eupatorium*, we may see similar acute differences between the weedy and nonweedy taxa in their reproductive biology and in their various other apparent physiological features. Reproductively, the weeds are characterized by a shortness of the vegetative phase between germination and flowering, by the relative independence of environmental controls on flowering, and by an economy of pollen production associated with self-pollination.

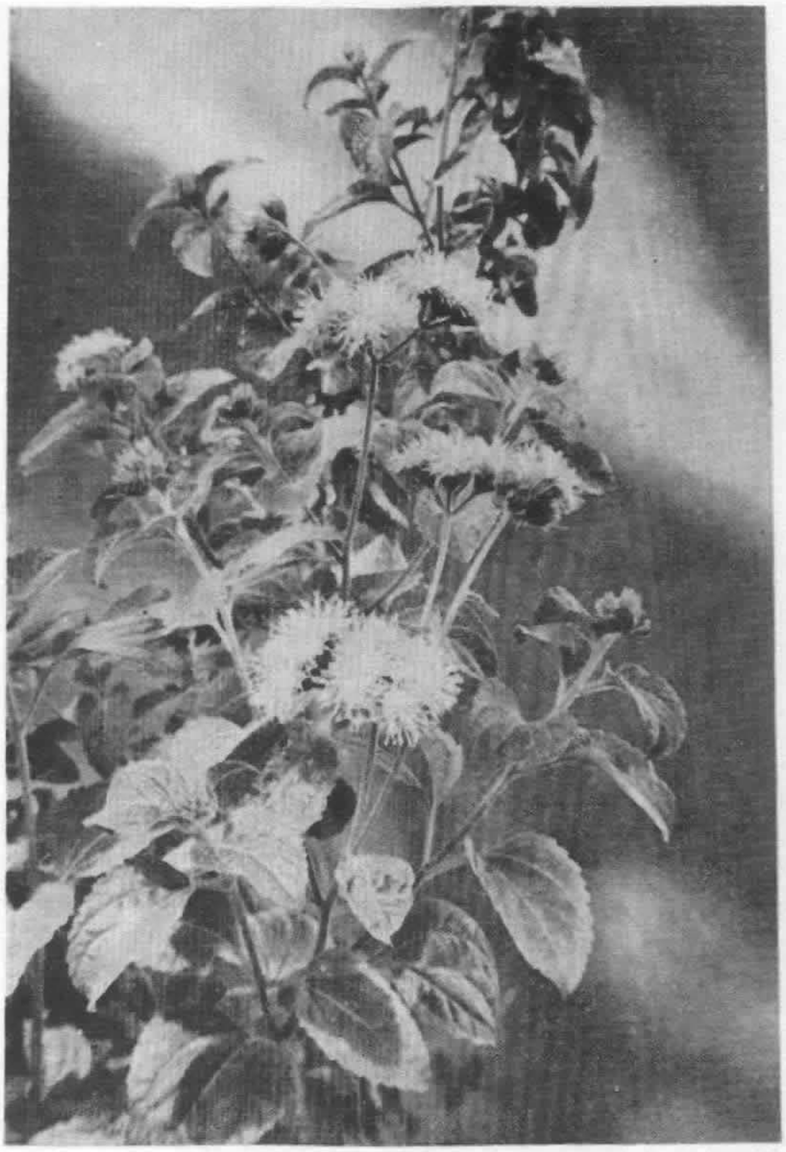

FIG. 5. Perennial, nonweedy *Ageratum microcarpum*, showing conspicuous blue flower heads.

The weeds show an annual, rather than a perennial habit, a wide environmental tolerance during growth, and striking developmental homeostasis (in the sense that they produce flowers and seeds successfully in a wide range of conditions). They also show plasticity in size in response to environmental variation (and, in this way, homeostasis and plasticity are not opposites). Their wide environmental tolerance is particularly striking in view of their prevailing self-pollination.

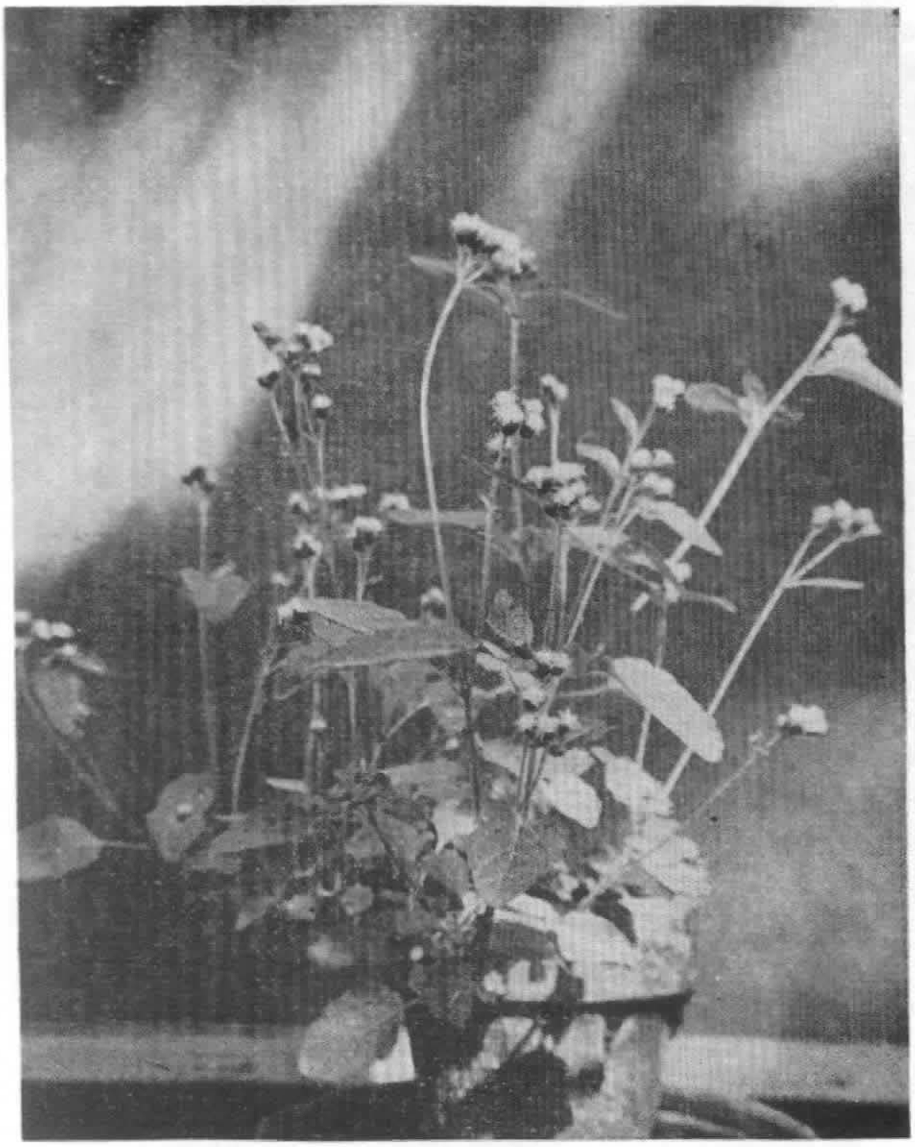

FIG. 6. Annual, weedy ***Ageratum conyzoides.*** About 10 plants crowded together in an 4-inch pot. Note small flower heads.

However, although the characteristics by which the weeds differ from the nonweeds are remarkably similar in both genera, the evolution of the weedy taxa has been achieved by quite different means chromosomally. Whereas *Ageratum conyzoides* is a tetraploid ($n = 20$), with 10 chromosomes homologous with those of its nonweedy relative, in *Eupatorium* the development of a weed from its nonweedy ancestor has been accompanied by a reduction in basic chromosome number from 20 to 4. This must have been one of the fastest reductions on record for these two morphologically very similar taxa may still be crossed easily, even with the self-incompatible one as the pistillate parent. Lewis and Crowe (1958) have shown that when a self-compatible form arises from a self-incompatible progenitor, subsequent evolution rapidly produces a situation in which crosses only succeed with the self-compatible form as the pistillate parent. In the *Eupatorium* hybrid the four large chromosomes from the weedy parent form as many multivalents with the smaller chromosomes from the nonweedy parent as their chiasma numbers will allow.

This contrast between *Eupatorium* and *Ageratum* should be borne in mind by anyone who would propound simple rules relating chromosomal changes to the development of weediness.

The characteristics which have been noted in the weedy species of *Ageratum* and *Eupatorium* are apparent in other taxa, too (Baker, 1954, 1958, 1959, 1962; Adams and Baker, 1962; Cumming, 1959). In particular, the wide environmental tolerance is to be seen, in some cases where there is reason to believe that only a single genotype is represented.

Thus, in 1958, I collected dandelion plants, *Taraxacum officinale* agg., at 9000-foot elevation on Mount Rose, in the Sierra Nevada, and carried them down to the University of California Botanical Garden, in Berkeley (elevation, 800 feet). The original plants are still growing and flowering vigorously in the Botanical Garden, and producing good seed, nearly 6 years after their original transplantation. Anyone familiar with the experiments carried out by Clausen and co-workers (1940) will know that subalpine ecotypes of native Californian plants subjected to the same treatment do not last very long in their new sea-level homes. This material of *Taraxacum officinale* is triploid ($3n = 24$), suggesting a hybrid origin.

Another odd-polyploid is *Oxalis corymbosa* DC. (Fig. 7). I have counted its chromosomes and they number 35, for it is a pentaploid on 7. Plants of *Oxalis corymbosa* never form seed for, not only are they pentaploid, but they represent only the short-styled form in a genus where tristyly with very strong self-incompatibility is characteristic.

Oxalis corymbosa is native to the American tropics and to the West Indies (Knuth, 1930); but, with man's aid, it has spread to the Old World and I have seen it growing well in the lowland tropics of Ghana, 4½° north of the Equator. I have also seen it, however, growing as a weed in Nottinghamshire, in England (53°N). The definitive comparison experiment needs to be done to prove that the plants from these climatically utterly dissimilar environments represent the same biotype, but the exclusively vegetative reproduction in this species suggests that, after its formation through an act of hybridization, there has been no opportunity for genetical recombination. The plants are certainly extremely similar morphologically.

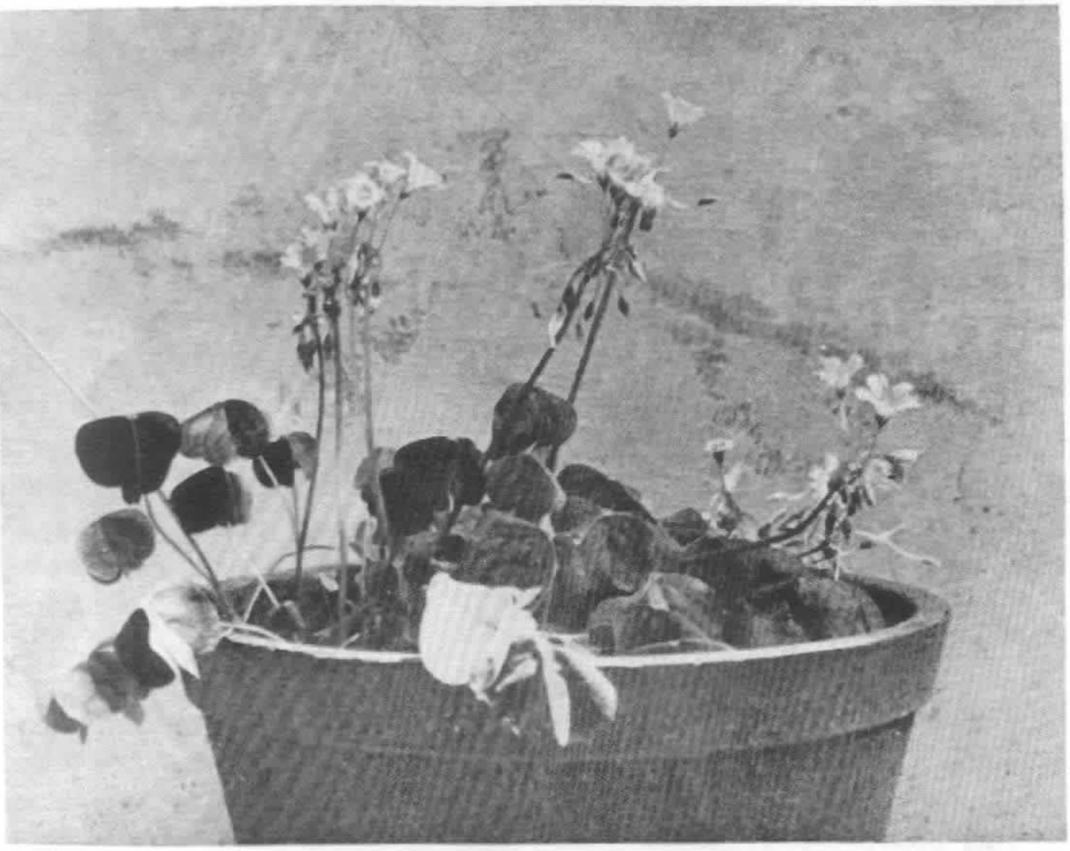

FIG. 7. Plant of *Oxalis corymbosa*, collected at Achimota, Ghana. The flowers are rose-colored.

Another rather different example of wide environmental tolerance in a weed, compared with its nonweedy relatives, may be drawn from the parasitic broomrape genus *Orobanche*. *Orobanche hederae* Duby and *Orobanche minor* Sm. are so closely related that some taxonomists have considered them conspecific (cf. Bentham and Hooker, 1924), yet *Orobanche hederae* is only found parasitic on ivy (*Hedera Helix* L.). *Orobanche minor*, on the other hand, although most often seen attached to legumes, is so catholic in its tastes that when Dr. A. D. Greenwood began to work with it in a greenhouse at the University of Leeds in England, the very light seeds flew everywhere, and plants came up attached to hosts as diverse as Pelargoniums, potted palms, and even *Psilotum*. There seems to be no limit to its range of potential hosts and I think that it is no accident that it is this species, *Orobanche minor*, rather than any of the species with a serious host restriction, which has become a successful weed in pastures in New Zealand, New York, and other lands far distant from its native Europe.

I suggest that the kind of genotype which provides the plant bearing it with a wide environmental tolerance, and gives it the ability to grow in a multitude of climates and edaphic situations, be referred to as a "general purpose" genotype. I shall further suggest that these "general purpose" genotypes are very frequently found in weeds.

Actually, for some perennial weeds, it seems that vigor and wide environmental tolerance, provided by such a genotype, may be more important than any ability of a plant to set seed.

For example, we may take the case of *Oxalis pes-caprae* L. (Fig. 8). This is the terribly badly named Bermuda Buttercup. It is not a buttercup and it is not from Bermuda. In its native South Africa, *Oxalis pes-caprae* occurs in several forms. One is a tetraploid (with 28 chromosomes), and another is pentaploid (with 35 chromosomes). Even in South Africa, plants which, from their morphology, appear to be pentaploid exhibit weediness (cf. Salter, 1962). Nevertheless, both the tetraploid and the pentaploid have been carried to the outside world as cultivated plants. The tetraploid escaped, however, from cultivation only in a few places (North Africa, India, and Australia), and it remains nonaggressive. In India it has been known from one station for 30 years (cf. Knuth, 1930; Mathew, 1958). In Australia it has been observed to be only spotty in its distribution, despite having all three style lengths represented in its populations, and reproducing by seed as well as vegetatively (Symon, 1961).

By contrast, the pentaploid has only vegetative reproduction by underground bulbils—it has never been seen to set a single seed for, like *Oxalis corymbosa*, in addition to being pentaploid, it has the further disadvantage of existing only in a short-styled form. Yet the pentaploid *Oxalis pes-caprae* has become a locally dense and serious weed in temperate and subtropical regions of Europe, eastern Asia, Africa, Australia, South America, and western North America. Actually it occurs along the paths outside our conference room here in Asilomar and is abundant in gardens and truck crop fields in coastal regions of California.

Pentaploid *Oxalis pes-caprae* has a rather wide climatic range and in the Botanical Garden at Berkeley it has withstood 9°F of frost without the slightest damage. It must have been formed by an act of hybridization as it is a pentaploid, presumably a hybrid between a tetraploid and a hexaploid, and it appears to be perpetuating the vigor which it got from this hybridization by its vegetative reproduction.

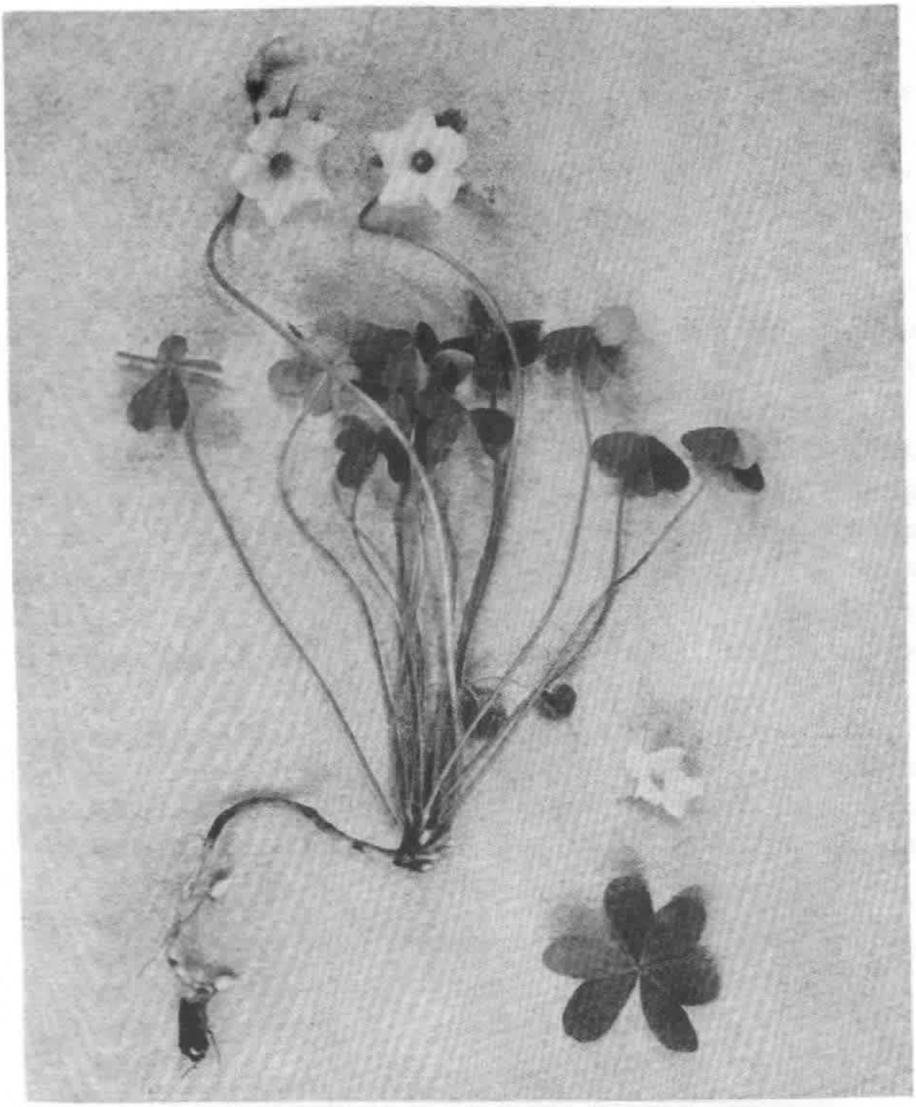

FIG. 8. Plant of *Oxalis pes-caprae,* collected at Berkeley, California. The bulb from which the present year's plant developed is shown, while two new bulbs are developing as offsets. The lemon-yellow flowers produce no capsules.

One of my students, Mrs. Jane Bock, is studying the behavior of Water Hyacinths (*Eichhornia*) in the Pontederiaceae. One of the species, *Eichhornia crassipes* (Mart.) Solms, is a dreadful weed which has spread with man's aid from its home in tropical South America to many other areas of the world, ranging from the tropics through the subtropics to merely warm-temperate central California. In California, near Stockton, it has to survive quite severe frosts each winter. Although most plants are killed by frost, enough escape for it to make a comeback the next summer. Such is the rate of growth under optimum conditions of uncrowded plants that *E. crassipes* may be blessed with one of the highest potential rates of organic productivity among the world's flowering plants (cf. Westlake, 1963).

Despite growing so successfully in this wide range of climatic conditions, *Eichhornia crassipes* rarely forms seeds and reproduces with their aid even more rarely. It appears to be self-incompatible and its very vigorous vegetative reproduction produces virtually sterile clones. Nevertheless, in Jamaica, where it has been introduced, it appears to be spreading more aggressively than a native species of the same genus, *Eichhornia paniculata* Solms., even though *E. paniculata* sets abundant seed (for it is self-compatible) and has vegetative reproduction as well.

At least in the two *Oxalis* cases, it looks as if heterosis, wide ecological tolerance, and developmental homeostasis may have been produced through an act of interspecific hybridization and then captivated by vegetative reproduction to serve the weed throughout its career. With this vigor and tolerance, these taxa have achieved success despite the absence or paucity of seed production. How much greater might their success have been if they were given all this *and* the opportunity to reach new areas by seed dispersal, too?

Of course, there are weeds in which the benefits of heterozygosity are preserved despite seed reproduction. It is well known that allopolyploidy provides one such means. The tetraploid weedy species of *Tragopogon* which Ownbey (1950) has been observing as they spread following their origin by hybridization and amphidiploidy near Pullman, Washington, are striking examples. The origin of *Ageratum conyzoides*, mentioned previously, is being investigated, and it probably was similar.

Another well-known mechanism for capturing the benefits of heterozygosity is through the preservation of translocation heterozygosity in the chromosomes by a balanced lethal system as in the subgenus *Euoenothera*, where many of the plants which show this system are weeds (Cleland, 1962).

A third, equally well-known circumstance in which heterozygosity may be preserved is by apomixis. By contrast to the purely vegetative apomicts which we have considered in the genus *Oxalis*, there are the many weeds which show agamospermy—seed formation without a sexual process being involved.

In the genus *Eupatorium* the most strikingly successful weed is of this nature. It is *Eupatorium adenophorum* Spreng. (Fig. 9). It is also known in the literature as *Eupatorium glandulosum* H. B. K. As Holmgren (1919) first showed (and I have confirmed), plants of this species are triploid (with 51 chromosomes) and form seeds without pollination. Embryo-sac formation follows diplospory and the unreduced egg nuclei then develop by diploid parthenogenesis. The tiny achenes produced by this agamospermous process serve for rather long-distance dispersal, while consolidation of the occupancy of an area is achieved by seed and by very vigorous vegetative reproduction.

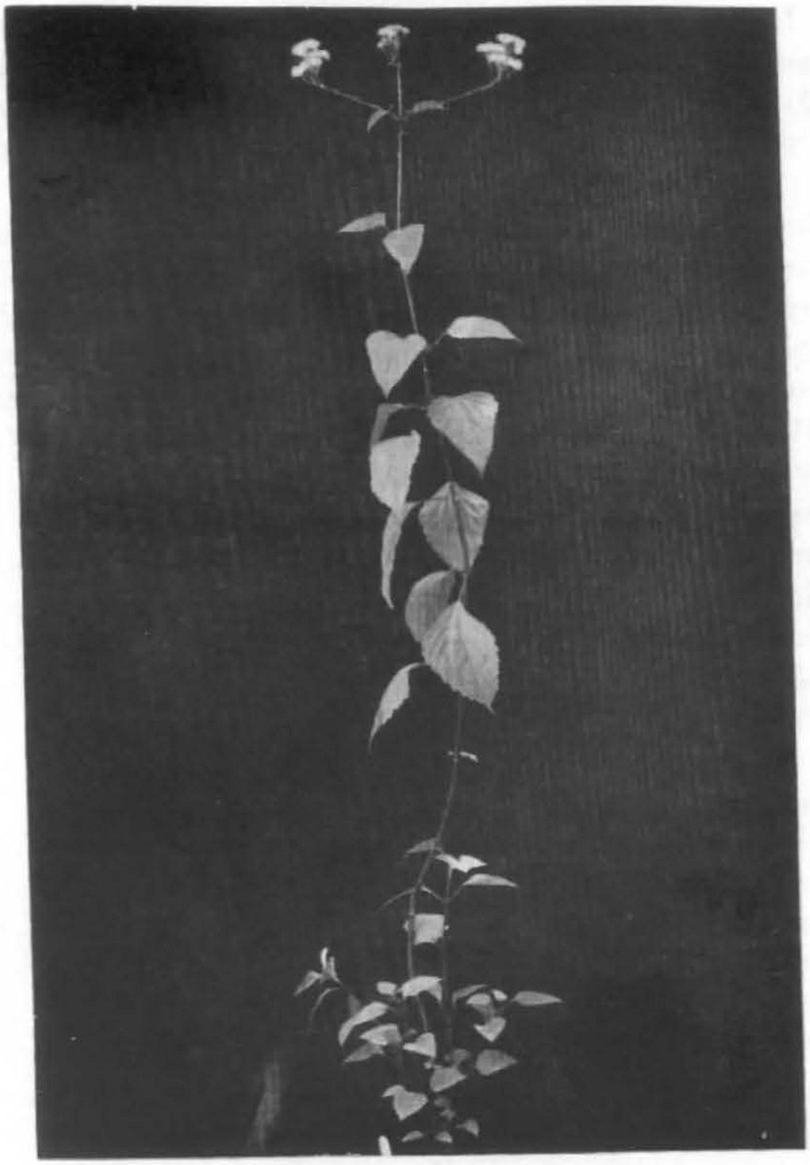

FIG. 9. Plant of *Eupatorium adenophorum* grown in the greenhouse in Berkeley from seed collected near Lucia, Monterey County, California. The white flower heads are borne at a height of 1 meter.

Such is the range of environmental tolerance in this species that it is well established from above 8000 feet in its native Mexico to tropical Jamaica and the subtropical rain forests of Hawaii, and from the aridity of the canyons near Pasadena to the foggy coast near San Francisco Bay. It is a serious weed in Australia, in India and in the Canary Islands. It has only recently been brought under control by biological control methods in Hawaii and Australia by using a stem-gall fly (Wilson, 1960). Its remarkable spread has been achieved even though genetical recombination must be at least very much slowed down by apomixis.

A similar wide range, apparently achieved without man's aid, is to be seen in the case of the fern *Polypodium dispersum* Evans. The remarkable life cycle of this fern is carried through entirely on one chromosome level, mitosis being substituted for meiosis prior to spore formation and new sporophytes being produced apogamously on the gametophyte (Evans, 1964). Once again the plants are triploid ($3n = 111$) and we may expect that it was an act of hybridization which produced the successful genotype.

This fern has achieved a distribution which reaches from Florida through the West Indies and tropical America to the Galapagos Islands. As the discoverer of this remarkable situation, Evans (1964, p. 263), pointed out, *P. dispersum* is remarkably stable morophologically throughout its range and "—in spite of its seemingly limited genetic potentialities, this somatic life cycle has evidently enabled the plant to become successfully adapted to its environment[s]."

Even without polyploidy, translocation heterozygosis, or apomixis, a "general purpose" genotype may be preserved by a high degree of self-pollination and a low number of chromosomes (as in the weedy *Eupatorium microstemon*). Even allelic diversity may be preserved in such a situation as this if there is some duplication of genes on a single chromosome, and this may be the case in *E. microstemon* where genes from 20 chromosomes (twice the basic number of 10) appear to have been brought together on only four chromosomes in the weed.

Thus, it does seem that "general purpose" genotypes, often apparently highly heterozygous, may serve weeds and other colonizing species well in providing a wide range of climatic and edaphic tolerance, enabling them to enter new areas. Ecotype formation may follow if their stay in the area is prolonged, but, because of their prevalent autogamy or apomixis, the weeds are apparently less well set up for rapid, fine local adaptation than are allogamous species native to the areas which the weeds invade.

When changes do take place after embarkation on a weedy life, some are such as to improve local adaptation, as Heiser (this Symposium) will be showing us in the sunflower genus, *Helianthus*, but others seem to be such as will increase general vigor and tolerance.

Thus, in the case of *Hypericum perforatum* L., the Klamath Weed, or St. John's Wort, Pritchard (1960) grew plants from seed collected from weeds in Australia, South Africa, Canada, and California. He grew them alongside plants raised from seed of the same variety (var. *angustifolium* DC) which had been collected in its native European area, whereupon the weedy plants showed themselves consistently more vigorous and taller growing. They produced more stolons in unit time and formed more flowers and more seed on each plant.

In an investigation recently completed at Berkeley, another student of mine, Dr. Costas Panetsos (1963), was able to show that the cultivated radish, *Raphanus sativus* L., which has escaped to become a weed, particularly around the coastal towns of California, has been assisted in taking up this weedy life by introgression from an already weedy species, *Raphanus raphanistrum* L. Apparently the flow of alleles from the weedy species has provided the one-time crop plant with a deeply penetrating taproot and a good supply of lateral roots, instead of the swollen, apparently inefficient "radish"-type root. In addition, the introgression has provided the erstwhile crop plant with rapid growth through the vegetative phase into flowering (reversing the effects of human selection for many centuries) and has given back to the plants a seed-dispersal system (for in the cultivated plant the indehiscent fruits tend not to separate from their pedicels and remain attached to the plant). Finally, a harder fruit wall is provided, rendering the seed less likely to be consumed by birds but assuring some measure of "dormancy" for the seeds before the wall rots away on the ground. With these aids, *Raphanus sativus* is becoming an abundant weed in some areas of the western United States and Canada.

If a newly introduced plant does not have appropriate "general purpose" genotypes available, it may be confined to a restricted area until these do become available through recombination or introgression. This may be one of the bases of the "lag" phase so often seen in the history of a new weed, although many other factors may also contribute to this delay in spread, such as the necessity to build up an "infection pressure" of propagules or the relaxation of a particular environmental deterrent (Salisbury, 1953).

The most famous example of a delayed spread in the British flora concerns the so-called "Oxford Ragwort," *Senecio squalidus* L. This species, of Sicilian or southern Italian origin, escaped from the Oxford University Botanic Garden before 1794, but was confined to old walls in the City of Oxford for very many years (Turrill, 1948). With the building of a railway between Oxford and London, it was enabled to spread slowly along the ballasted tracks toward the capital city. Its phenomenal spread throughout England has only come about in the last half century, and mostly since the bombings of World War II opened up new habitats for it.

Sir Edward Salisbury (1953) may be right in suggesting that it was necessary for a certain density of propagule production to be achieved before the explosive spread of this species could occur, but it is also very desirable that genetic comparisons should be made between the weedy material and the stocks from which it was derived to see if changes have occurred. Certainly the weeds have no special photoperiodic requirement, for plants can be seen in flower at any time of the year.

Although the plants are probably self-incompatible, Turrill (1948) reported that weedy London populations of *Senecio squalidus* are morphologically less variable than populations growing in the original area of introduction in Oxford, suggesting that not all genotypes were needed, or even useful, in the explosive spread of this weed.

If weeds can make good use of "general purpose" genotypes, why are similar "general purpose" genotypes not prevalent also in the nonweedy plants which have been investigated by genecologists?

Actually, Clausen, Keck, and Hiesey's experiments in California have shown that this kind of genotype can be produced by recombination following the crossing of ecological races in *Potentilla glandulosa* Lindl. (Clausen, 1949). When the F_2 from a cross between a foothill ecotype and a subalpine ecotype of *Potentilla glandulosa* was examined by growing ramets at Stanford, at Mather, and at Timberline, there were some plants, of course, which did better at one of the stations and some plants which were weak at all stations; but there were some plants which grew well (in the absence of competition) at all three stations. I should say that they possessed "general purpose" genotypes.

Similarly, in the genus *Poa*, following the artificial crossing of two facultatively apomictic taxa, *Poa ampla* Merr. and *Poa pratensis* L. var. *alpigena* E. Fries, a new strain of plants, also highly fertile and apomictic, was established which was unusually tolerant of wide differences in climate (Clausen, 1953). It grew vigorously in experimental gardens at latitudes ranging from San Fernando in southern California (at 34°N) to Volbu, in Norway (situated at 61°N and at 150-foot altitude). As Clausen (1953) says, "Such wide ranges of tolerance are not found in any other *Poa* in the wild." It must be emphasized that these experimentally produced forms with "general purpose" genotypes were never exposed to competition with other kinds of plant in a natural environment.

Clausen *et al.* (1951) had already pointed to the rather wide physiological tolerance of most races of *Poa pratensis* (verified by controlled greenhouse experiments). With the advantage of hindsight we can now remark that *P. pratensis* is the most successful colonizer among the species in the genus and its possession of "general purpose" genotypes may be related to this.

Generally, however, it seems that for nonweedy species, and particularly for those which grow in closed communities, such as perennial grasslands, adaptation through ecotypes of relatively limited tolerance but exquisite local adjustment is usually necessary for success in intense competition. The "general purpose" genotypes which can be selected artificially are not selected naturally here, for they produce plants which are "Jack-of-all-trades-but-master-of-none."

I suggest that in undisturbed communities, the natives, which are often allogamous, have appropriate breeding systems to produce finely adapting ecotypes through extensive recombination. On the other hand, weeds, to whom self-pollination or even apomixis is likely to be important for establishment after long-distance dispersal, or in building up a large population quickly whenever an opportunity presents itself, would be unable to produce recombinants as rapidly and, therefore, depend more obviously upon "general purpose" genotypes. These may preadapt them and help them to grow in a wide variety of climates and soils where a disturbance, usually man-made, has opened up the vegetation and has reduced competition. Generally, however, these weeds will be unsuccessful at entering the native vegetation wherein intense competition prevails.

It is noticeable that the few recently introduced weeds which have been successful in entering natural grasslands and other relatively undisturbed closed communities in the British Isles, have done so with the aid of vigorous vegetative reproduction. *Epilobium pedunculare* A. Cunn. and *Acaena anserinifolia* Druce from New Zealand and *Tetragonolopus maritimus* (L.) Roth. from the European continent have such creeping abilities, and all of them are grassland inhabitants in their native countries.

It is European experience that weed species seem most often to have been recruited from open habitats—seashores, the margins of salt marshes, rocky places in mountains, river banks, and the like. These are all habitats where "general purpose" genotypes and pioneering ability might already have proved advantageous.

On the other hand, equally open desert habitats—in the arid southwest of North America, for example—have not produced many weeds, perhaps because here genetic systems promoting a very fine adaptation have been favored, especially among the annuals, where germination is only called forth when very special sets of temperatures and rainfall come into conjunction and virtually assure the plants that they will have moisture enough to grow to maturity (Juhren *et al.*, 1956). This is another strategy and it is not one which preadapts a plant to life as a weed.

What has been said here for the origins of temperate weeds applies equally to the tropics. Repeated examples might be quoted of genera in which all species except one are extremely restricted in distribution, but the one exception has become a pantropical weed.

The genus *Tridax*, in the Compositae, shows this. It is restricted to the American tropics but, within that area, *Tridax procumbens* L. is the most widespread species. Thanks to man's help, *Tridax procumbens* is now spreading around the tropics of the Old World as well, even invading closed grasslands with its rapid and abundant seed reproduction as well as its creeping vegetative habit (Adams and Baker, 1962). *Ageratum conyzoides* is another example of an extremely successful weed which stands almost alone in a large tropical genus.

Within each of these genera, it seems that just one species has managed to hit the genetic jackpot. With the aid of a suitable reproductive system wherein propagules may be produced under a wide variety of conditions (without the need for specialized pollinators or even the presence of more than a single plant) and with suitable "general purpose" genotypes, this one taxon has needed only man's help in transportation and the opening up of closed communities to explode into world-wide weediness.

The Appendix contains a listing of characteristics which would seem to favor weediness in such taxa. Probably no existing plant has them all; if such a plant should evolve it would be a formidable weed, indeed.

APPENDIX

THE IDEAL (?) WEED

1. Has no special environmental requirements for germination.
2. Has discontinuous germination (self-controlled) and great longevity of seed.
3. Shows rapid seedling growth.
4. Spends only a short period of time in the vegetative condition before beginning to flower.
5. Maintains a continuous seed production for as long as growing conditions permit.
6. Is self-compatible, but not obligatorily self-pollinated or apomictic.
7. When cross-pollinated, this can be achieved by a nonspecialized flower visitor or by wind.

8. Has very high seed output in favorable environmental circumstances.
9. Can produce some seed in a very wide range of environmental circumstances. Has high tolerance of (and often plasticity in face of) climatic and edaphic variation.
10. Has special adaptations for both long-distance and short-distance dispersal.
11. If a perennial, has vigorous vegetative reproduction.
12. If a perennial, has brittleness at the lower nodes or of the rhizomes or rootstocks.
13. If a perennial, shows an ability to regenerate from severed portions of the rootstock.
14. Has ability to compete by special means: rosette formation, choking growth, exocrine production (but no fouling of soil for itself), etc.

REFERENCES

Adams, C. D., and Baker, H. G. **(1962)**. Weeds of cultivation and grazing lands. *In* "Agriculture and Land Use in Ghana" (J. B. Wills, ed.), Chapter 22. Oxford Univ. Press, London.

Baker, H. G. **(1948)**. Studies in invasion and replacement demonstrated by species of *Melandrium*. *J. Ecol.* **36,** 96–119.

Baker, H. G. **(1954)**. Research in Great Britain on species with weedy tendencies. Abstracted in *Rapp. et Comm. 8e Intern. Congr. de Botanique, Paris, 1954* Sect. 4, pp. 110–112.

Baker, H. G. **(1958)**. Studies in the reproductive biology of West African Rubiaceae. *J. W. Afr. Sci. Assoc.* **4,** 9–24.

Baker, H. G. **(1959)**. The contribution of autecological and genecological studies to our knowledge of the past migrations of plants. AIBS symposium paper, 1958. *Am. Naturalist* **93,** 255–271.

Baker, H. G. **(1962)**. Weeds—native and introduced. *J. Calif. Hort. Soc.* **23,** 97–104.

Baker, H. G. **(1964)**. Opportunities for evolutionary study in the tropics. *Taxon* **13,** 121–124.

Bentham, G., and Hooker, J. D. **(1924)**. "Handbook of the British Flora" (A. B. Rendle, ed.), *7th ed.* Reeve, London.

Clausen, J. **(1949)**. Genetics of climatic races of *Potentilla glandulosa*. *Hereditas* (*Suppl.*) pp. 162–172.

Clausen, J. **(1953)**. New bluegrasses by combining and rearranging genomes of contrasting Poa species. *Proc. 6th Intern. Grassland Congr., Univ. Park, Pa., 1952* pp. 216–221.

Clausen, J., Keck, D. D., and Hiesey, W. M. **(1940)**. Experimental studies on the nature of species I. Effect of varied environments on western North American plants. *Carnegie Inst. Wash. Publ.* **520.**

Clausen, J., Grun, P., Nygren, A., and Nobs, M. **(1951)**. Genetics and evolution of Poa. *Carnegie Inst. Wash. Yearbook 1950–1951* pp. 109–111.

Cleland, R. E. **(1962)**. The cytogenetics of *Oenothera*. *Advan. Genet.* **11,** 147–237.

Cook, S. A. **(1961)**. Aspects of the biology of *Eschscholzia californica* Cham. Ph.D. Thesis, University of California.

Cumming, B. G. **(1959)**. Extreme sensitivity of germination and photoperiodic reaction in the genus *Chenopodium*. *Nature* **184,** 1044–1045.

Evans, A. M. **(1964)**. Ameiotic alternation of generations: a new life cycle in the ferns. *Science,* **143,** 261–263.

Holmgren, I. **(1919)**. Zytologische Studien über die Fortpflanzung bei den Gattungen Erigeron und Eupatorium. *Kgl. Svenska Vetenskapsakad. Handl.* 59 (7), 1–117.

Juhren, M., Went, F. W., and Phillips, E. (1956). Ecology of desert plants. IV. Combined field and laboratory work on germination of annuals in the Joshua Tree National Monument, California. *Ecology* **37**, 318–330.

Knuth, R. (1930). Oxalidaceae. *In* "Das Pflanzenreich" (A. Engler, ed.), Vol. IV 130. Engelmann, Leipzig.

Lewis, D., and Crowe, L. K. (1958). Unilateral interspecific incompatibility in flowering plants. *Heredity* **12**, 233–256.

Mathew, P. M. (1958). Cytology of Oxalidaceae. *Cytologia (Tokyo)* **23**, 200–210.

Nelson, A. P. (1962). A genecological study in *Prunella vulgaris* L. (Labiatae). Ph.D. Thesis. University of California.

Nelson, A. P. (1964). Relationships between two subspecies in a population of *Prunella vulgaris. Evolution* **18**, 43–51.

Ownbey, M. (1950). Natural hybridization and amphiploidy in the genus Tragopogon. *Am. J. Botany* **37**, 487–499.

Panetsos, C. (1963). Sources of variation in wild populations of *Raphanus* (Cruciferae). Ph.D. Thesis, University of California.

Pritchard, T. O. (1960). *In* "The Biology of Weeds" (J. L. Harper, ed.). Black- pp. 130–139. Botanical Society of the British Isles, Oxford.

Salisbury, E. J. (1953). A changing flora as shown in the study of weeds of arable land and waste places. *In* "The Changing Flora of Britain" (J. E. Lousley, ed.), pp. 130–139. Botanical Society of the British Isles, Oxford.

Salter, T. M. (1962). *Oxalis pes-caprae.* Plate 1362 and accompanying text. *The Flowering Plants of Africa* **35**(1/2).

Sims, J. (1815). No. 1730. *Ageratum coelestinum. In* "Curtis's Botanical Magazine." Sherwood, Jones, London.

Sims, J. (1823). No. 2524. *Ageratum mexicanum. In* "Curtis's Botanical Magazine." Sherwood, Jones, London.

Swanson, J. R. (1964). *Claytonia (Montia) perfoliata,* a genecological and evolutionary study. Ph.D. Thesis, University of California.

Symon, D. E. (1961). The species of *Oxalis* established in South Australia. *Trans. Roy. Soc. S. Australia* **84**, 71–77.

Turrill, W. B. (1948). "British Plant Life." Collins, London.

Westlake, D. F. (1963). Comparisons of plant productivity. *Biol. Rev. Cambridge Phil. Soc.* **38**, 385–425.

Wilson, F. (1960). "A Review of the Biological Control of Insects and Weeds in Australia and Australian New Guinea." Tech. Comm. No. 1. Commonwealth Institute of Biological Control, Commonwealth Agricultural Bureaux. Farnham Royal, England.

Discussion of Paper by Dr. Baker

Lewontin: Have any experiments been done in which a weedy species and a closely related nonweedy species are put in a plot without any cultivation? I am thinking of experiments to show that the weedy species will not outdo the locally adapted type by actually bringing the seeds of the weedy species in and competing with the locally adapted type.

Baker: Obviously this is something worth doing. There are Harper and Sagar's experiments with *Plantago*.

Harper: Yes, and some Hungarian work by J. P. Nagy which has just been done. Nagy measured what he called "ecesis-resistance."

Waddington: How long does a weedy species succeed in being dominant in a place? You get a weedy vegetation covering an area if it is left alone; will this come to a climax assemblage and stay there for good?

Baker: I think it depends to what extent the area has been altered. As far as California grasslands are concerned, it is inconceivable that they would ever go back to being the native bunch grasses and a few annuals that they were, because the seed sources of the native grasses have gone now. Even if the hand of man were removed from California, I doubt very much if the grasslands would change for some time.

Waddington: The present vegetation contains general purpose genotypes, but would you eventually get back again to a climax vegetation which has become closely adapted?

Baker: I should think so and I should think that the presently occurring weeds might actually be the ancestors to the plants that would later on show this different kind of adaptation.

Harper: I think it is perhaps a little unfair for an agriculturist to comment on a paper by the director of a botanic garden—but it seems to me that it is worthwhile to point out how potentially dangerous botanic gardens are. There are not only deliberate and repeated introductions of the same species to the same area year after year to build up an inoculum but also usually in order beds the deliberate placement of congeners side by side, giving perfect conditions for the creation of polyploid races, hybridization, introgression, etc. I do wonder, in this context, whether one might find more valid evidence, more easily analyzable evidence, of rates of change in plant species by looking at botanic garden material than looking at weeds. I say this because so often in botanic garden material, one knows precisely the place of origin and one knows precisely the period of time for which the plants have been cultivated. Also strains of the same origin have been cultivated in a number of places. By contrast, for most of our weed floras, we have only vague indications of where they came from, and very often only quite vague information of how long they have been here.

Baker: Yes, I think it could be one further stage of refinement. But, unfortunately, botanical gardens have not been run with this in mind and so sometimes their accession records are not too good.

Harper: The release of *Salvinia* into Ceylon rice fields has become catastrophic, and again this came from a botanic garden.

DeBach: I wonder if you would consider including in your ideal weed list the lack of natural enemies, because we have cases where weeds are now no longer weeds because they have natural enemies. If this were overlooked or not considered, you would have situations where you actually have a potential weed, but you might evaluate it as a nonweedy species. This is the case for Klamath weed now in northern California and *Opuntia* in Australia.

Baker: Yes, actually I did think of putting down resistance to fungal pests and so on. Perhaps I should include resistance to all kinds of parasites, pests, and so on.

Stebbins: It seems to me that in the Mediterranean area nothing could become a weed unless it could resist cattle, sheep, goats, donkeys, cows, and women that cut the wood!

Purseglove: In a survey of the weeds on our experimental farm at the University in Trinidad, we have recorded 250 species and of these, nearly 80 species are mentioned in Darlington and Wylie's "Chromosome Atlas." Of those 80 species, 50 are polyploids. It is just to add evidence to what's been said. A lot of these are, of course, annual species.

Ehrendorfer: From your calculations of the prerequisites for an ideal weed and from what you told us about the very different cytogenetic types which are found among weeds, one would conclude that a weed might develop from practically all cytogenetic systems and patterns of differentiation. I am not sure yet whether this conclusion is in line with all of the data.

Baker: I think it is possible that this could be true because there is evidence of weeds having arisen in virtually all of these circumstances. I doubt that any weed in existence has all of the characteristics that I put in my list. If it did, it would take over the world. Therefore, there must be compensations. Some species which have become weedy have several strikes against them but they have, on the other hand, several very positive characteristics as weeds. I'm thinking of the white campion (*Silene alba*) in this respect. Here is a plant which is dioecious and I would not have expected dioecism to be good for weediness. But white campion managed to get around the world pretty well in the days when cereal grain, grass seed, and ballast were not inspected as well as they are now. Masses of seeds were distributed instead of single seeds and, as a consequence, the dioecism was no barrier to its spread that way. In other cases—in *Raphanus*, for example, where whole fruits are dispersed—self-incompatibility does not pose the disadvantage that it might in a species where seeds are distributed singly. We planted whole fruits of *Raphanus sativus* just to see what would come up. Several seedlings came up together, but they did not compete with each other so destructively that only one would come to maturity. In fact, we would get four or five plants growing very close together, forming a reduced number of flowers, it is true, but nevertheless able to cross-pollinate each other. Thus, there are all sorts of compensations which are possible and, as a consequence, I do think that almost any kind of plant might give rise to a weed.

Ehrendorfer: My question was mainly concerned with the cytogenetic patterns of differences like stabilization at the diploid level, getting dysploid (aneuploid) reduction of base numbers, or polyploidy.

Baker: Well, I know from reading your abstract that you believe that there are such trends in various groups, and I agree with you. The point I would simply make is that they are not absolute. In this case *Ageratum* and *Eupatorium* are such closely related genera that I have made intergeneric hybrids between them. And yet, the evolution of weediness seems to be going on in two different cytogenetic ways in those two closely related genera: polyploidy in one, reduction of the base number in the other.

Zohary: I think that there are definite trends which you could perhaps express as follows. When you take weeds and you find very frequently that they are self-pollinated, it is significant that you find that their close relatives which are not weeds are not self-pollinated plants and are self-incompatible. So this is a sort of generalization we could make. But we couldn't make the generalization that weeds are always selfers. When you take polyploid groups, you'll find that many weeds are actually members of polyploid groups and then the tendency, with several exceptions for sure, will be that you will find that the majority of the weedy types are polyploids but perhaps several of the diploids are also weedy. But you have many, if the group is nonweedy, cases where the diploid entities are not weedy and the polyploid entities are almost all exclusively weedy. But you can't generalize and say weeds are polyploids or weeds are selfers. If one should put it in such a way, I think we'll have a good picture of this situation which we find.

Baker: Certainly.

Mayr: I would like to get back to the basic theme of our conference. Listening to what I've heard about weeds—surely they are colonizing species in a way because they get around a great deal, but I have begun to wonder what their future is. Most of what the weeds are doing is making them highly successful in disturbed habitats, but, at the same time, this facilitates all sorts of mechanisms which maneuver them more and more inevitably successfully into dead-end streets so to speak. If they remain cross-fertilizing then they have a highly panmictic set up which is contrary to an evolutionary future; if they become apomictic or self-compatible or something like this their gene complexes pretty well stabilize and also deprive them of an evolutionary flexibility. I am just wondering whether, as an evolutionist, one should not look for colonizing species among rather ordinary species that do not look very different from other noncolonizing species. Let us say, as I mentioned yesterday, the mountain species in the Malay archipelago that managed to jump across many barriers to the new monsoon forest in Timor. Looking at these species in Malaya, I would not have pegged a single one as having any particular capacity for colonizing, and yet they did it very successfully. When we think of colonization we must avoid being misled into believing that the species which do the most spectacular things at the present time—like the weeds—are the typical colonizers and that they have a particularly bright evolutionary future. As a matter of fact, I rather suspect that the future of such species is, on the whole, rather dim.

Baker: I think I agree with you with regard to their future; however, I am reminded of what was mentioned yesterday, that most colonizations by any kind of organism are unsuccessful in more than just a very short term. Maybe weeds are no worse than the others. There are species like *Spartina townsendii* which have come out of what was originally a weed colonization. One species of *Spartina* (*S. alterniflora*) came to Europe. This species of *Spartina* hybridized with another one (*S. stricta*) and out of that has come an amphiploid (*S. townsendii*) which has a very definite future. So maybe in a small proportion of these cases there is going to be a successful taxon which will be perpetuated in a long-term basis.

Harper: I think soon we are going to run into trouble if we should equate weeds with colonizing species. Weeds are plants which are recognized by being a niusance to one or another of man's activities. These are not necessarily colonizing species; they may just represent natural vegetational succession—the return of the original flora after man has disturbed it. And to try and find biological characteristics and unity in biological characteristics among those plants which are a nuisance to man is a very different thing from trying to find a unity in those colonizing organisms which have high invading ability.

Stebbins: Well, it seems to me that you can't expect to find a unity in all species that have a high colonizing ability because the first requisite of colonization is adaptation to the habitat. And adaptation to human habitats is going to be quite different from adaptation to other habitats.

Baker: (delayed comment brought forward for relevance) I should point out that I define weeds on the basis of their colonization of habitats disturbed by man, not on their nuisance value.

Stebbins: I want to make a couple of comments on what Ernst Mayr just said. In the first place, I think he said in passing that a greatly *panmictic* species has no future. I will challenge that on the grounds that it could always pass through a new bottleneck and have a new future. This could apply if you have a weedy species spread over a very large area, with a very large panmictic population, and it has evolved races adapted to a diversity of environments.

Mayr: Well, I said it only with respect that if a species had this tremendous dispersal facility so that it can get anywhere then it will have trouble developing these peripherally isolated populations that we believe are important.

Stebbins: It may have trouble for some time, but this big habitat which is here now will become smaller in future geological ages when the environment changes. Then the new cycle will begin.

Waddington: To me the most interesting question raised by Baker's talk is why all plants don't have these highly successful general purpose genotypes; his point being that they don't have them because these general purpose genotypes only pay off well in quick returns. They can spread and make enormous populations, but they don't seem to be suitable for incorporation in a permanent vegetation.

Baker: That's right. They are "Jack-of-all-trades-but-master-of-none." They don't give the finest local adaptation.

Waddington: Therefore it seems to me that the most interesting thing about weeds is not how they spread but how they eventually disappear and are supplanted by something that is more permanent.

Baker: This is what Lewontin was suggesting that we should be studying and I agree with him that we should.